BUD BANK DENSITY REGULATES INVASION BY EXOTIC PLANTS

By

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CHAPTER I

INTRODUCTION

Grasslands and savannas cover as much as 30-50% of the earth's ice-free land area and provide valuable goods and services to humans (Ellis and Ramankutty 2008) while functioning as habitat for plants, animals, fungi, and microbes. Like other ecosystems, grasslands and savannas are affected by elements of global environmental change, including biological invasions. Biological invasions in grasslands and savannas may be regulated in part by bud banks, an underappreciated feature of these ecosystems, which enables rapid resource capture by native plants following a disturbance or resource enrichment event. The purpose of the research I report in this thesis was to evaluate the role of bud banks in regulating invasions by exotic plants.

In this chapter I review aspects of grassland, bud bank, invasion, and resource ecology relevant to the greenhouse microcosm study I completed to test the role of bud banks in regulating exotic plant invasions. The second chapter of this thesis is a concise, manuscript style report of this greenhouse microcosm experiment which will be submitted to an academic journal for publication, with forthcoming revisions and contributions by Gail W.T. Wilson and David C. Hartnett.

GRASSLANDS

Climate significantly influences the distribution of grassland and savanna ecosystems worldwide (Holdridge 1947, Whittaker 1975). In North America, grasslands occupy most of the

central part of the continent, as well as large portions of other regions. Within these grasslands, climate further influences species composition and productivity. Mean annual precipitation in central North America increases along a gradient from west to east, producing a shift from desert grasslands and shortgrass prairies in the xeric west to tallgrass prairie in the mesic east. Mean annual temperature decreases from south to north, resulting in a decrease in the dominance of C_4 species along a gradient from south to north (von Fischer et al. 2008). Net primary productivity in the grasslands on central North America increases from west to east, and is generally higher in the mid and southern latitudes than in the north (Knapp and Smith 2001, NTSG 2004).

Climate, weather, herbivory, and fire disturb grasslands and savannas on time scales ranging from days to years, and are key drivers of biological diversity and habitat heterogeneity in these ecosystems (Milchunas et al. 1988, Briggs and Knapp 1995, Roques et al. 2001). However, these disturbance agents are not independent of each other. Primary production in grasslands responds strongly to variations in precipitation (Knapp and Smith 2001). Weather influences fire ignitions and behavior, and herbivory and fire are intimately linked (Fuhlendorf and Engle 2001).

Herbivory by invertebrates, small mammals, and large mammals is a constant feature of grassland ecosystems. Herbivore stocking rate, animal species and type (e.g. sex, age), and timing of herbivory determine the effect of herbivory on individual plants and communities. In the Great Plains of North America, native bison (*Bison bison*) and domesticated cattle (*Bos taurus*) prefer grasses and preferentially graze regrowth which may occur following a disturbance event (Reppert 1960, Coppedge and Shaw 1998). It has been documented that bison generally graze this regrowth intensively, with a mean residual height of about four centimeters (Pfeifer and Hartnett 1995). When grazing intensity is not high this preference results in a spatially heterogeneous pattern of non-grazed and repeatedly grazed patches (Weaver and Tomanek 1951, Ring et al. 1985, Fuhlendorf and Engle 2001). Grazing animals also discriminate between plants of different species and developmental stages, and cause non-grazing effects such as trampling, trailing,

wallowing, and urine deposition. Clipping and mowing treatments are similar to herbivory by large mammals in that they defoliate plants, but are much more uniform than grazing (Vinton and Hartnett 1992). Some of the same traits which enable populations of plants native to grasslands to persist under herbivore pressure (e.g. sheltered growing points) also enable these species to persist in habitats that experience frequent fire.

Aboveground primary production that is not consumed by herbivores accumulates as standing biomass or litter, which decomposes or accumulates on the soil surface. Under dry environmental conditions accumulated biomass can be ignited by lightning or humans and burned. Immediately following a fire regrowth in burned landscape patches may be heavily grazed by large herbivores, and with increasing time since fire grazing pressure diminishes as less palatable and less fire-tolerant plants become more common (Fuhlendorf and Engle 2001). Fire controls plant composition by killing plants which lack adaptations sheltering meristems and/or conducting tissues (e.g. cambium) from the intense heat of a fire (e.g. encroaching woodland vegetation), and by promoting regeneration of fire adapted species through resource release or other processes.

BUD BANKS

Vascular plants reproduce sexually through flowering and seed production, and vegetatively through tillering, sprouting, and other asexual processes. Meristems associated with rhizomes and other belowground perrennating organs compose the bud bank (*sensu* Harper 1977), which contributes to plant recruitment in most plant communities. Despite their ubiquity, relatively few empirical studies have directly investigated the role of bud banks in the dynamics of populations, communities, landscapes, or ecosystems (Mullahey et al. 1991, Hay and Newman 1996, Hendrickson and Briske 1997). In contrast, the ecology of seed banks has been well studied (Fenner 1985, Baskin and Baskin 1998).

Bud banks are more important than seed banks as a source for plant recruitment in many grasslands (Thompson and Grime 1979, Glenn-Lewin et al. 1990, Pyke 1990, Hartnett and Keeler 1995, Hartnett and Fay 1998, Benson et al. 2004). For example, seed banks in tallgrass prairie may be large (> 6000 seeds $m^{-2;}$ Weaver and Mueller 1942, Rabinowitz 1981), but establishment of seedlings of dominant grasses from seed is rare and episodic (Christiansen and Landers 1966, Glenn-Lewin et al. 1990). Even in grazed or disturbed tallgrass prairie the majority of new plant recruitment arises from the bud bank, and not from seed (Rogers and Hartnett 2001). In contrast, both seeds and bud banks are important sources of recruitment in more arid grasslands where bud bank densities are lower and soil disturbances and gap dynamics play important roles (Coffin and Lauenroth 1988, 1989, 1990, Fair et al. 1999). However, the relative importance of these two recruitment mechanisms and the frequency of successful seedling establishment in the semiarid grasslands of the Great Plains and southwestern United States remain controversial (Lauenroth et al. 1994) and unknown for grasslands in other regions.

Precipitation significantly influences patterns of bud bank density. Along a precipitation gradient in the Great Plains extending from desert grassland to tallgrass prairie, bud bank density was shown to increase with mean annual precipitation, which accounted for 80% of the variation between sites (Dalgleish and Hartnett 2006). In 2004, the year Dalgleish and Hartnett (2006) sampled, mean bud bank density in the desert grassland site was 146 ±24 meristems/m² (mean ±1SE) and as high as 2450 ±231 meristems/m² at their most mesic tallgrass prairie site. Additionally, seasonal changes in grass bud banks driven by the formation, initiation, and mortality of buds were similar across a several-fold range in mean annual precipitation and productivity: densities were highest in March, decreased in June, and rose slightly in September.

Bud bank density is also influenced by management, particularly by burning and grazing. In tallgrass prairie, fire and grazing have been shown to have opposite effects on bud bank density (Benson and Hartnett 2006, Dalgleish and Hartnett 2009); frequent fire promoted high bud bank density, and persistent grazing depleted bud banks. These studies of fire and grazing

indicate that the management history of rangelands, in addition to environmental characteristics, will determine bud bank size.

The response of grasslands to environmental changes such as variations in resource availability may be limited by bud bank demography (Benson et al. 2004). In some grasslands variation in net productivity may be driven more strongly by bud bank dynamics and resultant tiller densities than by variation in growth of individual tillers (Knapp and Smith 2001, Benson et al. 2004). This observation has led to speculation on the potential ability of bud banks to regulate resource levels and biological invasions (Dalgleish and Hartnett 2009).

BIOLOGICAL INVASIONS

Geological evidence indicates that life on Earth began approximately 3.85 billion years ago (Mojzsis et al. 1996), about 650 million years after the formation of the Earth and perhaps only 50 million years after the surface of the earth cooled enough to form a solid crust. Since that time organisms have spread throughout the seas and across the terrestrial surface of the Earth and evolved into the many species of microbes, fungi, plants, and animals now present on the Earth (Darwin 1859). Individuals and populations of these species actively or passively disperse throughout their environment until they reach a community where species interactions limit their fitness or a barrier such as a sea, desert, or mountain range which prevents further range expansion. Occasionally, propagules (i.e. seeds, rhizomes, eggs, spores, juveniles, adults, etc) of a species disperse beyond these barriers without human intervention and establish viable populations in a new region of the world. Thus, biological invasion is a natural (i.e. not strictly anthropogenic) process that has been occurring for billions of years. However, the frequency of biological invasions has dramatically increased as a result of human activities (Lockwood et al. 2007). For example, prior to the arrival of humans the Hawaiian Islands likely received one new plant species every 100,000 years, but following the arrival of humans the frequency of

colonization by new plant species has risen to the current average of one species every 22 years (NRC 2002, Lockwood et al. 2007).

The process of biological invasion is similar to the process of succession (Davis et al. 2001). In both primary and secondary succession species already present in the local/regional species pool enter habitats and biotic communities from which they were formerly absent. In contrast, biological invasion involves species not from the local/regional species pool, but from the global species pool entering biotic communities. Thus, the disciplines of invasion ecology, which emerged as a field of study in the late 20th century, and community ecology, with a much longer history, are closely related and scientists working in these fields study many of the same phenomena (Davis et al. 2000, 2001).

The community ecology concept of ecological filters applies to biological invasions; there are many barriers to the successful colonization of one region of the globe by species from another. As a result, only a fraction of the species from one region becomes invasive in another (Williamson 1996, Jeschke and Strayer 2005). Barriers to invasion are associated with each of the stages of the invasion process: transport, establishment, and spread (Lockwood et al. 2007).

The transportation stage of the invasion process involves the movement of propagules from one region to another. In the absence of human participation, such long distance dispersal may involve the movement of species by strong winds or ocean currents. Human activities have strongly affected the transportation of species, as well as other stages of the invasion process (establishment and spread). In many cases exotic species are deliberately sought out and brought to areas outside of their native ranges (e.g *Pennisetum ciliare*, Hanselka 1988), and in other cases exotic species are accidentally introduced into new habitats (Mack 2004). The historic and current growth of international trade, tourism, and motorized vehicle travel are responsible for the coincidental, documented increase in the rate of transportation of species to habitats outside of their native ranges. Not only has the frequency of transportation increased, but also the speed of

transport has increased as human technology has advanced, potentially increasing the probability that propagules survive the transportation stage.

Propagules of an exotic species may either perish before reproducing or survive and reproduce in the new habitats that they enter. Exotic species establish themselves in these new habitats when immigration or reproduction rates are high enough to sustain a population. To establish an exotic species must be able to survive in the climate of the receiving habitat, and in cases where immigration rates are too low to sustain a population all of the resources the species needs to complete its lifecycle must be present in that habitat. Additionally, higher numbers of exotic propagules arriving in a new habitat increase the probability that enough individuals will survive predation, damage, and competition to find the resources needed to grow and establish a population (Lockwood et al. 2005).

In the spread stage, established exotic species reproduce and expand their range throughout the landscape. Spread is essentially an ongoing repetition of the transport and establishment stages occurring at a smaller scale. Traits associated with high mobility may promote the spread of non-native species (e.g. high reproduction rate, wind dispersed seed). Biological invasions affect ecological patterns and processes in the spread stage, but not all invading species have large effects on the invaded community (Vitousek et al. 1996, Williamson 1996).

Thus, the success of a species in invading a new habitat appears to depend on at least three factors: propagule pressure, species traits, and habitat invasibility (Lonsdale 1999, Barney and Whitlow 2008). Consequently, understanding patterns and mechanisms of biological invasions requires consideration of each of these factors, which is difficult to accomplish in observational field studies. As a result, small-scale assembled communities that afford researchers control over propagule pressure, species traits, and habitat invasibility are often used to study invasion ecology (e.g. Davis and Pelsor 2001, Gross et al. 2005).

Propagule pressure is the number of propagules of an exotic species arriving in a habitat outside of their native range. Propagule pressure depends on both the number of propagules transported in a single event, and on the number of times propagules are transported to the receiving habitat. Higher propagule pressure arising from large and/or frequent species transport events correlates with higher invasion success (Lockwood et al. 2005). However, populations of non-native species may originate with a single individual of a species capable of parthenogenesis, apomixis, vegetative spread, or another form of asexual reproduction.

Species traits, including reproductive strategy, are the product of the selective pressure a species has experienced in the past. In the context of invasion ecology the term "species trait" refers to any characteristic of a species, such as reproductive strategy, resource use efficiency, photosynthetic pathway, or the production of defensive compounds and structures. Non-native species equipped with allelopatic chemicals, the ability to fix nitrogen, or other adaptations previously absent from the communities they enter may become successful invaders in large part because of these adaptations (Callaway and Aschehoug 2000). The fitness of non-native species may also improve in their non-native range where they experience comparatively little predation/herbivory and are able to devote a higher proportion of their resources to growth and reproduction (Blossey and Notzold 1995).

Some habitats are more susceptible to invasion than others (Elton 1958, Davis et al. 2000, Davis and Pelsor 2001, Lockwood et al. 2007). The absence of predators, herbivores, and pathogens of an exotic species in a biotic community may permit or increase invasion (Keane and Crawley 2002), while the absence or scarcity of resources prevents or limits invasion. Charles Elton hypothesized that the richness of a community is negatively related to invasibility because rich communities theoretically utilize more of the available resources in a habitat (1958). This "Biotic Resistance Hypothesis" has been heavily researched and debated, and remains controversial because of conflicting evidence (Fridley et al. 2007). Mark Davis and colleagues (2000) argue that resource availability regulates plant community invasibility irrespective of

species richness, and that increases in resource availability associated with resource enrichment and/or decreased uptake by resident plants increase susceptibility to invasion (the "Fluctuating Resources Hypothesis").

RESOURCES

In ecology, a resource is defined as anything that is consumed (in an economic sense) by an organism with the result of improved fitness (Tilman 1980). By this definition four classes of resources exist: physical space, chemical resources (Lavoisier 1789), light (Mayer 1845, Govindjee and Krogmann 2004), and biological resources (Udovic 1981).

Chemical resources are used by organisms to meet nutrition and hydration needs. Organisms obtain chemical resources in elemental form or in compounds taken up from the atmosphere, soil, water, and other organisms. Macronutrients which plants require in greater abundances include H, C, N, O, Mg, P, S, K, and Ca (Singer and Munns 2006). Micronutrients including B, Cl, Mn, Fe, Ni, Cu, Zn, Mo, and sometimes Na, Si, Co, and Se are required in lesser amounts (Singer and Munns 2006).

Photosynthetic organisms require light to form carbohydrates from carbon dioxide and water, and all other organisms, except chemoautotrophs, ultimately depend upon carbohydrates produced by photosynthetic organisms for energy. In plant communities light intensity is highest at the top of the canopy and is reduced as light passes through the canopy. At high light intensities photosynthesis is not limited by light. However, at ground level, where seedlings emerge, average light intensity may fall below the level needed to meet respiration demands for energy (the "light compensation point", Chapin et al. 2002), leading to mortality of heavily shaded plants.

Organisms that perform essential services for organisms of another species function as biological resources. Pollinators, mycorrhizal fungi, and other symbionts are important biological resources. For example, at least 80% of the world's plant species are known to form mycorrhizal relationships (Wang and Qui 2006), and some plant species cannot reproduce in the absence of biological resources (e.g. *Ficus spp.*, Murray 1985; warm season grasses in tallgrass prairie, Wilson and Hartnett 1998).

Scarcity of resources limits the growth and reproduction of organisms; because of stoichiometric requirements the resource available in the lowest relative quantity limits growth (the "Law of the Minimum"). Light, moisture, and nitrogen limitations frequently restrict plant growth (Knapp and Seastedt 1986, Knapp and Smith 2001), but the low availability of any nutrient or resource may limit plant growth. Fluctuations in resource levels associated with disturbance events, seasonal changes in availability and uptake, and resource enrichment events cause shifts in resource limitation and thereby influence biological diversity (White and Pickett 1985, Davis et al. 2000).

Organisms living in close temporal and physical proximity interact directly or by affecting resource levels in their environment, and dead or dormant organisms may continue to alter their environment and thereby interact with other individuals (D'Antonio and Vitousek 1992). Biological interactions take a variety of forms, depending on the effects (beneficial, neutral, or detrimental) of the interaction on the two individuals involved (Holmgren et al. 1997): mutualism (+, +), predation/parasitism/herbivory (+, -), commensalism (+, 0), neutralism (0, 0), amensalism (-, 0), and competition (-, -).

Resource-Ratio theory (Tilman 1980, 1982) is based on a connection between resource uptake and resource supply. According to the theory, species are not able to occur where resource scarcity or utilization by other organisms causes resource concentrations to fall below the levels needed by the species to grow (Tilman 1980, Wilson et al. 2007). Recent review of Resource-

Ratio theory (Miller et al. 2005, Wilson et al. 2007) affirms the validity of the theory, though much of the supporting evidence is from trials examining unicellular organisms.

Like Resource-Ratio theory, the Fluctuating Resources Hypothesis (FRH) proposed by Mark Davis and colleagues (2000) is based on resource uptake and resource supply, and has emerged as a leading theory of plant community invasibility. In the decade between the publication of the FRH in 2000 and the present (July 2010) it has been cited in at least 672 scientific articles (ISI Web of Science), featured prominently in textbooks (e.g. Lockwood et al. 2007), and referenced in other documents. According to the FRH, plant communities are more susceptible to invasion when resource availability increases due to resource enrichment and/or decreased uptake. The FRH is based on four fundamental ecological principles already discussed in this chapter: 1) plants require resources to grow, survive, and reproduce; 2) resource supply is limited; 3) individual plants of different species interact; and 4) resource availability within a defined area varies with time.

Although the FRH is frequently cited and widely accepted as a theory of not only plant community invasibility but also of habitat invasibility generally, few studies have tested the predictions of the theory. The few studies that have tested the FRH have been conducted in mesic grassland and old field plant communities (e.g. Davis et al. 2000, Davis and Pelsor 2001), and the theory is largely untested in other systems and with other types of organisms.

SYNTHESIS

Elements of global environmental change including biological invasion are affecting grasslands worldwide. Bud banks present in grasslands potentially regulate habitat invasibility through resource preemption, but this hypothesized relationship is based on the predictions of the Fluctuating Resources Hypothesis (Davis et al. 2000), a theory that has not yet been thoroughly tested. The greenhouse microcosm experiment reported in the following chapter tests the role of buds banks in regulating plant invasions.

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CHAPTER II

BUD BANK DENSITY REGULATES INVASION BY EXOTIC PLANTS

INTRODUCTION

Bud banks, the analogue of seed banks comprised of dormant meristems on rhizomes and other structures (*sensu* Harper 1977), play an important and little-studied role in the ecology of both woody and herbaceous perennial plants. Bud banks enable vegetative reproduction, facilitate rapid regrowth following disturbance events such as fires, and permit seasonal dormancy in herbaceous perennial plant species (Dalgleish 2007). Strategies and life histories of species that maintain bud banks differ, and the size and function of the bud bank varies from one community to another (Lauenroth et al. 1994, Lehtila 2000). In the prairies of central North America, bud bank density increases with mean annual precipitation along a gradient extending from the desert grasslands (146 ±24 meristems/m², mean ±1SE, as measured in 2004) in the west to the tallgrass prairies of the east (2450 ±231 meristems/m²; Dalgleish and Hartnett 2006). In tallgrass prairie ecosystems as much as 99.4% of total plant recruitment throughout the growing season has been shown to originate from the bud bank (Benson and Hartnett 2006). Therefore, bud banks play an important ecological role in tallgrass prairie ecosystems (Rogers and Hartnett 2001, Benson et al. 2004).

Grassland ecosystems experience frequent disturbance. Historically, climate, weather, fire, large mammalian herbivores, and smaller herbivores such as prairie dogs (*Cynomys spp)* and Orthopterans were the primary disturbance agents operating in grasslands and savannas worldwide (Milchunas et al. 1988; Briggs and Knapp 1995; Roques et al. 2001). Although fire regimes have been modified, native bison (*Bison bison*) have largely been replaced by domestic cattle (*Bos taurus*), and prairie dogs have been eradicated throughout much of their former range, disturbance remains important in the grassland ecosystems of central North America. Moreover, in the past century disturbances associated with off-highway vehicle use, oil and gas exploration and development, road and utility line construction, and "range improvement" projects (e.g. stock tank construction) have become common. Disturbances may create "windows of opportunity" for biological invasions to occur (Myster 1993), and the frequent disturbances grasslands experience may provide ample opportunity for exotic species establishment and spread.

Intentional and accidental introductions of exotic species from distant regions of the globe have become increasingly common as technology and market forces have stimulated international trade and tourism (Lockwood et al. 2007). Commercial, recreational, and even natural resource management activities initiate and accelerate biological invasions into new habitats across the entire surface of the earth. Few regions are completely free of invasive species, and all habitats appear to be vulnerable to biological invasion (Vitousek et al. 1996). While many exotic species do not substantially affect ecological patterns or processes in their introduced range, some non-native species have a profound effect on the ecology of native systems.

Biological invasion success depends on at least three factors: propagule pressure, species traits, and habitat invasibility (i.e. the susceptibility of the habitat to invasion; Lonsdale 1999). Each factor may be targeted in biological invasion prevention campaigns and in exotic species control efforts, or, alternatively, in intentional introduction campaigns (e.g. the development of buffelgrass cultivars, seedbed preparation prior to post-fire seeding). Because each of these factors must be accounted for in comparative studies of invasion success– and because of ethical

barriers to intentionally introducing exotic species to new habitats– observational studies and broad-scale, long-term experimental field studies of invasion success are problematic. Thus, controlled environment studies are valuable tests of mechanisms potentially influencing habitat invasibility (Fraser and Keddy 1997).

The susceptibility of grasslands to invasion by exotic plants may be related to bud bank densities in these habitats (Dalgleish and Hartnett 2009). The Fluctuating Resources Hypothesis (Davis et al. 2000) predicts that the susceptibility of plant communities to invasion increases when resource availability increases following a change in resource use or resource enrichment. Theoretically, high bud bank densities enable rapid reductions in the availability of unused resources and strong negative interactions with plants reproducing from seed, and thus potentially reduce invasibility and render habitats more stable than they would be with lower bud bank densities (figure 1). Furthermore, because reduced plant densities permits larger plant size and correspondingly higher individual resource uptake, the relationship between bud bank density and invasibility is likely non-linear, with a threshold of invasibility at low or intermediate bud bank density. If this hypothesized relationship between bud bank density and invasibility truly exists, communities with higher bud bank densities are more stable (resistant to change).

In this study I tested the hypothesis that maintaining large bud banks enables resident vegetation to rapidly preempt resources following disturbance under three levels of simulated herbivory (clipping). Grazing and mowing are common in grasslands, and as a form of disturbance recurring at intervals shorter than the seasonal replenishment of bud banks potentially alter the role of bud banks in regulating plant invasions.

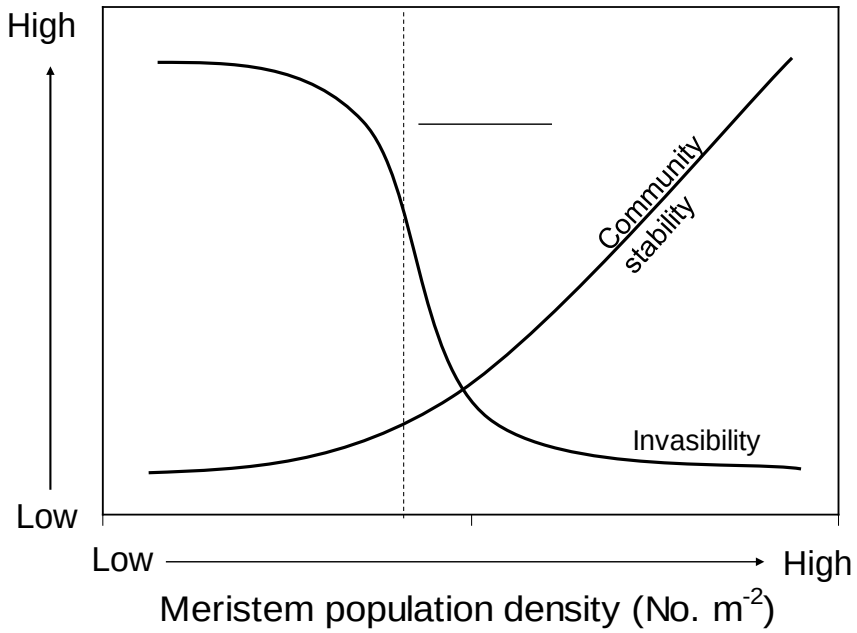

Figure 1. Hypothesized relationship between bud bank density, invasibility, and community stability.

MATERIALS AND METHODS

I tested the role of bud banks in regulating invasion by exotic plants in a greenhouse microcosm experiment. The microcosms measured 32 cm (width) x 42 cm (length) with a surface area of 0.13 m², and were filled to a depth of 20 cm. I established bud bank densities equivalent to 0% (0 meristems/m²), 30% (approximately 750 meristems/m²), 60% (approximately 1500 meristems/m²), and 100% (approximately 2500 meristems/m²) of average native tallgrass prairie field density (Dalgleish and Hartnett 2006). Patches with each of these levels of bud bank density are present in grassland landscapes. Microcosms were also subjected to one of three levels of simulated grazing: no clipping, moderate intensity clipping (clipped to 4 cm height every 28 days), and high intensity clipping (clipped to 4 cm height every 14 days). One replicate of each of the twelve treatments was placed within each of six randomly arranged blocks within the greenhouse (72 microcosms total).

Microcosms were housed in a climate controlled fiberglass greenhouse located in Stillwater, Oklahoma, USA. Throughout the experiment, temperature and relative humidity within the greenhouse tracked ambient conditions closely, though the greenhouse was consistently slightly warmer than the ambient air. The fiberglass panels of the greenhouse allowed a maximum of 56% of ambient photosynthetically active radiation to enter the greenhouse, based on repeat measurement taken with a ceptometer on 19-20 May, 2009. No shade cloth was used during the experiment.

I collected native tallgrass prairie soil on 28 February, 2009 at Konza Prairie Biological Station (KPBS), which is located approximately 13 km south of Manhattan, Kansas, USA on native tallgrass prairie in the Flint Hills of eastern Kansas. Prior to the start of the microcosm experiment this soil was passed through a 6 mm sieve to remove biological material and repeatedly mixed to homogenize the soil. By thoroughly mixing the soil I evenly distributed seeds already in the non-sterile soil across treatments and blocks.

I collected rhizomes of the dominant, native tallgrass species *Andropogon gerardii* (big bluestem), *Panicum virgatum* (switchgrass), and *Sorgastrum nutans* (Indiangrass) on 27 February and 6 March, 2009 at KPBS. I washed the soil from the rhizomes and sorted rhizomes by species. The sorted rhizomes were then packed in moist vermiculite, and placed in a 4 ºC cooler to keep the buds viable and dormant until experimental setup.

I filled each microcosm with 25 L of sieved and mixed soil on 8 April, 2009. I watered the soil as it was added to each microcosm, thereby achieving both settling of the soil and wetting of the entire soil column. On 6 May, I removed all seedlings that germinated from the soil seed bank and placed rhizomes of the three native species (*A. gerardii*, *P. virgatum*, and *S. nutans*) into the microcosms at a depth of 6-10 cm. I added rhizomes in the ratio of 3 *A. gerardii*: 2 *S. nutans*: 1 *P. virgatum*, a ratio typical of the occurrence of these species at our collection site at KPBS. A total of 60 rhizomes were placed in a uniformly-spaced arrangement in 100% density microcosms, 36 in the 60% density microcosms, and 18 in the 30% density microcosms. One

week later, I sowed seeds of *Bothriochloa ischaemum* (old world bluestem, a perennial C_4 caespitose grass), *Bromus japonicus* (Japanese brome, an annual C_3 grass), and *Lespedeza cuneata* (sericea lespedeza, a leguminous perennial forb/sub-shrub) into each microcosm at a rate equivalent to 300 viable seeds/m²/species. *B. ischaemum, B. japonicus,* and *L. cuneata* are highly-successful, non-native invaders of the tallgrass prairie region and together possess a broad range of species traits. Over the duration of the experiment, the soil was kept moist as I periodically watered microcosms to field capacity.

Fourteen days after the exotic seeds were sown into the microcosms, all native and emerged non-native plants in both moderate and high intensity clipping treatments were clipped to a height of 4 cm, based on the observation that bison and cattle preferentially graze regrowth intensively (Reppert 1960; Coppedge and Shaw 1998), to a height of approximately 4 cm (Pfeifer and Hartnett 1995). After this first clipping, microcosms subjected to moderate intensity clipping were clipped every 28 days and microcosms subjected to high intensity clipping were clipped every 14 days.

To evaluate invasion success I monitored the emergence (detectable germination), establishment (plants surviving beyond the seedling stage), survivorship (live plants at the end of the growing season), and reproduction (plants reaching reproductive status) of invasive plants within each microcosm. To track emergence, establishment, survivorship, and reproduction I conducted a count of the number of individuals of each exotic species plus any accidentally introduced species (i.e. those originating from the soil seed bank) in each microcosm every 14 days. I also measured the standing aboveground biomass of native and exotic plants at the end of the growing season (22 weeks after exotic seeds were sown into microcosms). I clipped all plants at ground level, separated these by species and reproductive status, and obtained the oven dry weight (48 h @ 60 ºC) of each sample to determine standing aboveground biomass. Bud bank density treatments were monitored by counting the number of native tillers in each microcosm 21 days after rhizomes were added.

This greenhouse microcosm experiment employs a randomized, complete-block design. Data were compared statistically via analysis of variance (ANOVA), Duncan's post-hoc procedure, with a critical value of 0.05.

RESULTS

Exotic species:

Emergence: Emergence of exotic plants ranged from 42.4 ± 5.6 (95% confidence interval) to 85.6 ± 15.7 percent of the seed sown into each microcosm (table 1). Both bud bank density and clipping significantly influenced emergence ($P<0.001$ and $P= 0.014$, respectively). In contrast to my hypothesis, emergence was generally facilitated by higher bud bank density. Clipping tended to reduce emergence.

Establishment: Between 89.2 ± 5.1 and 99.7 ± 0.5 percent of emerged plants were able to survive beyond the seedling stage (table 1). Bud bank density influenced the establishment rate of exotic plants ($P<0.001$) but clipping did not ($P=0.813$). As with emergence, I observed higher establishment at greater bud bank densities, in contrast to my hypothesis.

Survivorship: Bud bank density did not strongly influence the survival of established exotic plants throughout the growing season ($P=0.265$), but clipping did ($P=0.001$). Clipping at either moderate or high intensity generally promoted survivorship. Survivorship ranged from 57.9 ± 6.5 to 81.7 ± 6.0 percent (table 1).

Reproduction: Bud bank density did not strongly influence the percentage of surviving exotic plants reaching the reproductive stage ($P=0.834$). In the absence of clipping, 26.2 ± 5.1 to 43.2 ± 8.8 percent of surviving plants flowered (table 1). The percentage of surviving exotic plants reaching the reproductive phase was also strongly influenced by clipping ($P<0.001$): clipping at either moderate or high intensity reducing the number of surviving exotic plants that entered the reproductive stage to a similar level across all bud bank densities.

Aboveground biomass: The total aboveground biomass of exotic plants ranged from 25.62 ± 2.64 to 664.72 ± 65.05 g/m² (table 1). Both bud bank density and clipping strongly influenced exotic aboveground biomass ($P<0.001$ for each). As predicted by my hypothesis, in the absence of clipping exotic aboveground exotic biomass was 675% higher at the lowest bud bank density than at the highest. Clipping at either moderate or high intensity reduced the aboveground biomass of exotic plants to a similar level at all bud bank densities.

The total aboveground biomass of plants which reached the reproductive stage of development (i.e. flowering) was likewise strongly affected by bud bank density ($P=0.001$) and clipping ($P<0.001$). Among non-clipped treatments, the biomass of reproductive exotic plants was 875% higher at the lowest bud bank density than at the highest (table 1). The biomass of reproductive-stage plants was similar for all clipped treatments (moderate and high intensity).

Native species:

Tiller density: After 3 weeks, I observed 787 ± 95 native tillers/m² at the highest bud bank density, 503 ± 52 at our 60% bud bank level, and 276 ± 41 at our 30% bud bank level. The mean tiller density at the 60% level was 64% of the mean tiller density at our 100% level, and mean tiller density at the 30% level was equivalent to 35% of the mean tiller density at our 100% level.

Biomass: Bud bank density and clipping both affected the production of aboveground biomass by native plants ($p=0.008$ and $p<0.001$, respectively). At our highest bud bank density (100% of the estimated field density) native plants produced 414.88 ± 53.58 grams of aboveground biomass / m² (table 1). At our 60% bud bank density level native plants produced 76% of this amount, and at 30% bud bank density they produced 68% of the aboveground native plant biomass produced at our highest bud bank density. Previous research has shown the long-term (23 year) mean aboveground biomass in native tallgrass prairie is 442.6 ± 22.4 g/m² (mean ± SE, Knapp and Smith 2001).

Treatment		Measures of Exotic Species Success						Natives
Bud Bank Density (%)	*Clipping Level*	*Emergence (% Seed)*	*Establishment (% Emerg.)*	*Survivorship (% Est.)*	*Reproduction (% Surv.)*	*Reproductive Biomass (g/m²)*	*Aboveground Biomass (g/m²)*	*Native Aboveground Biomass (g/m²)*
0	No Clip	63.8 ± 9.2^{b}	94.3 ± 4.6^{abc}	62.3 ± 4.7^{de}	43.2 ± 8.8^{a}	627.22 ± 78.26^{a}	664.72 ± 65.05^{a}	-
	Moderate	42.4 ± 5.6^{c}	89.2 ± 5.1^{c}	72.6 ± 6.5^{abcd}	1.2 ± 1.5^{d}	4.79 ± 8.38^{d}	50.53 ± 3.75^{de}	-
	High	43.9 ± 3.5^{c}	90.1 ± 4.3^{c}	81.7 ± 6.0^{a}	1.3 ± 2.0^{d}	2.67 ± 5.23^{d}	41.90 ± 6.92^{e}	-
30	No Clip	67.9 ± 9.1^{b}	92.7 ± 3.4^{bc}	69.7 ± 5.2^{bcd}	36.0 ± 3.8^{b}	139.00 ± 31.21^{b}	170.45 ± 35.25^{b}	281.66 ± 48.91^{c}
	Moderate	58.1 ± 11.9^{bc}	93.3 ± 4.0^{bc}	64.0 ± 7.9^{cde}	0.4 ± 0.8^{d}	2.64 ± 5.18^{d}	34.09 ± 6.04^{e}	19.21 ± 1.75^{d}
	High	67.3 ± 8.1^{b}	93.9 ± 2.8^{bc}	70.3 ± 8.5^{bcd}	0.3 ± 0.6^{d}	1.65 ± 3.23^{d}	37.41 ± 5.85^{e}	7.58 ± 2.62^{d}
60	No Clip	85.6 ± 15.7^{a}	96.8 ± 2.6^{ab}	57.9 ± 6.5^{e}	26.2 ± 5.1^{c}	72.84 ± 28.68^{c}	102.36 ± 35.79^{c}	315.90 ± 30.98^{b}
	Moderate	69.0 ± 13.8^{ab}	96.7 ± 3.1^{ab}	73.7 ± 6.5^{abc}	2.6 ± 2.0^{d}	1.49 ± 1.15^{d}	29.71 ± 6.85^{e}	24.32 ± 5.57^{d}
	High	66.1 ± 11.0^{b}	96.8 ± 1.8^{ab}	72.5 ± 5.6^{abcd}	1.3 ± 2.5^{d}	2.03 ± 3.99^{d}	33.38 ± 7.27^{e}	11.78 ± 5.00^{d}
100	No Clip	74.3 ± 12.3^{ab}	96.2 ± 2.8^{ab}	68.6 ± 3.6^{bcd}	32.7 ± 6.0^{b}	64.30 ± 12.14^{c}	85.70 ± 15.47^{cd}	414.88 ± 53.58^{a}
	Moderate	72.1 ± 9.0^{ab}	97.9 ± 2.2^{ab}	78.1 ± 4.5^{ab}	0.9 ± 1.3^{d}	0.67 ± 1.05^{d}	25.62 ± 2.64^{e}	40.08 ± 6.41^{d}
	High	65.9 ± 15.6^{b}	99.7 ± 0.5^{a}	72.7 ± 11.1^{abcd}	4.2 ± 4.1^{d}	3.03 ± 2.56^{d}	36.02 ± 6.99^{e}	20.23 ± 2.72^{d}
p-value:	D x C	*<0.001*	*0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
	Density	*<0.001*	*<0.001*	*0.265*	*0.834*	*0.001*	*<0.001*	*0.008*
	Clipping	*0.014*	*0.813*	*0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
	Block	*0.222*	*0.961*	*0.216*	*0.975*	*0.999*	*1.000*	*0.999*

Table 1. 95% confidence intervals for indicators of the growth of three exotic species (*Bothriochloa ischaemum*, *Bromus japonicas*, and *Lespedeza cuneata*) seeded into microcosms with different native plant (*Andropogon gerardii*, *Panicum virgatum*, and *Sorgastrum nutans*) bud bank densities. Superscripts indicate statistical similarity, within columns (one-wayANOVA, Duncan's post-hoc, α=0.05).

DISCUSSION

The results of this greenhouse microcosm experiment support the hypothesis that maintaining large bud banks enables resident vegetation to rapidly preempt resources following disturbance, thereby limiting the "window of opportunity" and reducing the susceptibility of the community to invasion by exotic plants. Although native plants originating from the bud bank may act as nurse plants and promote exotic emergence and establishment, the aboveground biomass of reproductive invasive plants and total aboveground biomass of invasive plants were negatively related to bud bank density. The relationship between bud bank density and exotic biomass I observed is nearly identical to the theoretical relationship I proposed prior to experimental testing (figure 1). Moreover, our data suggest the existence of an invasibilty threshold at a point between 0 and 30% (800 meristems/m^2) of the estimated mean field bud bank density at KPBS. Above this threshold I believe sufficient numbers of native meristems break dormancy and grow into new tillers to largely monopolize available light, moisture, and/or chemical resources, thereby limiting the growth of the invasive species. The production of aboveground biomass by invasive plants in microcosms with the highest bud bank density (2500 meristems/m^2) was limited almost as much by resource preemption by the native plants as it was by continuous clipping.

Continuous clipping, at either moderate or high intensity, limited the growth and reproduction of the exotic species included in this study, but it also limited the growth and reproduction of the native grass species included in this study. However, continuous clipping carried out for many years would likely suppress bud bank densities and thereby ultimately increase the susceptibility of a plant community to invasion (Dalgleish and Hartnett 2009). Clipping has been shown to produce similar results as grazing in tallgrass prairie grasses (Vinton and Hartnett 1992). However, there are certainly potential differences between grazing of plants

under field conditions and clipping under greenhouse conditions, so I recommend the results of this portion of our study be interpreted with caution.

All habitats appear to be susceptible to biological invasion, including those with large bud banks. The flora of the tallgrass prairie region, which has comparatively high mean bud bank density (Dalgleish and Hartnett 2006), includes exotic species (Smith and Knapp 1999). The three exotic species included in this study possess traits that, in combination with their intentional and accidental introduction, have allowed them to become common, ecologically and economically important invasive species of tallgrass prairie ecosystems. In our study, the bud bank of native tallgrass species imparted stability to tallgrass plant communities by significantly limiting the growth and reproduction of even these successful invaders, but it did not prevent invasion completely. In consequence, exotic species may be able to persist at low abundance in communities with high bud bank density until conditions become favorable to population growth and spread, at which point they will become more successful invaders.

The results from our study indicate restoring and maintaining plant communities with high bud bank densities will assist land managers in limiting and regulating plant invasions, as I observed lower invasibility of communities with higher bud bank densities. Climate, fire, and grazing all influence bud bank densities in tallgrass prairie and fire and grazing may be managed to maintain high bud bank densities: frequent burning increases and maintains high bud bank densities by promoting grasses, while persistent grazing depletes bud banks by promoting forbs and bare ground (Benson and Hartnett 2006, Dalgleish and Hartnett 2006, Dalgleish and Hartnett 2009). Additionally, land managers may make more effective use of limited resources by focusing invasive species detection and control efforts on landscape patches with lower bud bank densities.

Experimental microcosms are simplified, model ecosystems which afford researchers precise control over experimental treatments and environmental variables, but may not adequately address questions of scale and complexity (Fraser and Keddy 1997). By employing this approach

in this study, I avoid the issues of landscape heterogeneity, potentially unequal propagule pressure arising from the uncontrolled dispersal of exotic propagules by animals and abiotic agents, and ethical barriers to introducing exotic species into new habitats. Theory (Tilman 1980, Davis et al. 2000), preliminary field observations, and the ability of the bud bank to regulate the success of the highly invasive species used in this study suggest that the findings of this study may be reliably applied in the study and management of grasslands. Further research comparing bud bank density and invasion success in multiple regions will improve our understanding of the role of bud banks in regulating plant invasions.

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Pages in Study: 32 Candidate for the Degree of Master of Science

Major Field: Natural Resource Ecology and Management

Scope and Method of Study: Grasslands and savannas, which cover as much as 30-50% of the earth's ice-free land area, are affected by global environmental changes including biological invasions. To test the role of bud banks, an important feature of native prairie communities, in regulating invasion by exotic plants under three levels of simulated grazing (no clipping, 28 day clipping interval, and 14 day clipping interval) I conducted a greenhouse microcosm study. Using native rhizomes planted into native prairie soil, I established bud bank densities of 0, 30, 60, and 100% of mean tallgrass prairie bud bank density. Seeds of three exotic species were sown into each microcosm. The number of emerging and established exotic plants in each microcosm was counted every 14 days. I measured the aboveground biomass of each species at the end of the growing season (22 weeks). Assessments of exotic plant emergence, establishment, survivorship, reproduction, and biomass based on these measurements were compared using analysis of variance.

Findings and Conclusions: The effects of the bud bank on exotic plant emergence, establishment, and survivorship were inconsistent and relatively weak. However, reproduction and biomass of exotic species were strongly influenced by bud bank density. In the absence of clipping, the biomass of exotic species was 675% higher at the lowest bud bank density than at the highest density. Furthermore, I found evidence for an invasibility threshold between 0-30% of mean field bud bank density in tallgrass prairie. These findings improve our understanding of plant invasion and suggest that restoring and maintaining bud banks should be a priority for land managers seeking to prevent and limit plant invasions.

ADVISER'S APPROVAL: Gail Wilson